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Pelargonium (Geraniaceae) and the long-tongued fly pollination guild: coevolution and polymorphism in a specialized pollination system

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Abstract

In South Africa, a group of long-tongued flies and the flowering plants they pollinate form a unique and diverse pollination guild system almost entirely endemic to the Greater Cape Floristic Region. This system makes up only a small portion of the biodiversity of the Region, but it is likely a key to understanding the evolutionary processes that have lead to the observed biodiversity. Aside from its unusual pollinators, this guild system is of particular interest due to the extremely labile morphology of both the fly species and the associated flowering plant species, which geographically vary significantly in proboscis lengths and floral traits, depending on the species composition of the local community. This leads to remarkable polymorphic diversity within an otherwise obligately mutualistic system. In this paper, information about long-tongued flies and their pollination system is collected, reviewed and synthesized. The floral guild system, especially the focal genus *Pelargonium,* is also reviewed, given the high percentage of *Pelargonium* species that are obligately or facultatively pollinated by long-tongued flies. A revision to the pollination guild system is suggested by introducing the sub-guild concept. Additionally, the patterns of adaptive shifts and morphological changes within the guild system are analyzed as they relate to reciprocal adaptation, coevolution, and the process of ecological speciation within this highly-endemic, biodiverse region of South Africa. This synthesis indicates that this specialized pollination mutualism may maximize pollination efficiency in a continually shifting biotic and abiotic environment. More intense specialization and perhaps eventual speciation likely occurs only where both the pollinators and the associated floral guild species exert continuous selection pressure on each other over time. Additionally, new venues of study are suggested in order to better understand the genetic and environmental bases for adaptive shifts within the pollination guild system system.

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Introduction

Long-tongued flies and the flowering plants which they pollinate form a co-evolved pollination system in South Africa of relatively recent focal study; although they were first observed as pollinators in 1908 by Marloth, they have only been studied as a significant, coevolved pollination system since the 1980s (Goldblatt & Manning 2000). This unique pollination system consists of a pollinator guild of long-tongued flies, species in the families Tabanidae and Nemestrinidae known for their elongated proboscises, and an associated guild of flowering plants, with many members belonging to one of two families of flowering plants, the Iridaceae and the Geraniaceae. The genus *Pelargonium* in the latter is of note for having a large proportion of long-tongued fly-pollinated species: at least 25% of species are pollinated exclusively by these flies (Struck 1997). Several other plant families are represented in the floral guild, but not in as high proportions of component species as the above two families. The long-tongued fly pollination system is almost entirely contained within a large, diverse, highly-endemic biogeographic region, comprising both the Cape Floristic Region and the Succulent Karoo of South Africa, together called the Greater Cape Floristic Region (Born et al. 2007). The overall impact of the long-tongued fly pollinator guild is small relative to the great diversity of the flowering plants and their associated pollinators in the region. Long-tongued flies are few in number, both in species diversity and population density, with a relatively small overall range along the southern and western coasts. Fewer than 200 plants are confirmed to depend on long-tongued flies exclusively as obligate pollinators (Goldblatt & Manning, 2000). However, within that dependent group of plants, the long-tongued fly pollination guilds are vital. Seed set and successful pollination rates decline in these species when not visited by their specific fly pollinators (Johnson & Steiner 1997; Anderson & Johnson 2008), making the long-tongued flies an important, keystone species in the region. In addition, recent studies have suggested that long-tongued flies are in fact opportunistic pollinators that visit additional flowers

outside of those with which they share an obligate mutualism. Multiple species of flowers that display typical traits of the long-tongued fly pollination syndrome have been observed to be visited by other species of insect pollinators in environments where long-tongued flies are less common (de Merxem et al. 2009; Anderson et al. 2010). This suggests a more complex set of community interactions rather than an exclusive mutualism between pollinator and plant species. A recent study by Pauw and Stofberg (2008) even indicates that the long-tongued flies may be subject to selective pressures from multiple species of differing host plants, resulting in adaptations evolved for maximum pollination efficiency across multiple species of plants in a process they call "diffuse coevolution." By this token, the long-tongued fly pollinator guild may actually involve more facultative pollination, in addition to a variety of obligate pollination relationships within the associated floral guild. This loose interdependent mutualism, where both pollinator guild and floral guild have coevolved specific traits, but are also often capable of adapting to other non-dependent species, results in a high amount of intraspecific variation among locations and communities within both guilds (Struck 1997; Andserson and Johnson 2008; Pauw and Stofberg 2009). Understanding the pollination system, including the pollinator and floral guilds, may provide new insights into the process of coevolution and the process of speciation within the Greater Cape Floristic Region, for which this system serves as a useful model. The long-tongued fly pollination system as a whole is thought to be vulnerable to extinction as a consequence of the specialization of both pollinator and plant guilds (Goldblatt and Manning 2000), especially those species engaged in obligate pair mutualisms. Indeed, one long-tongued fly species is already suspected to be extinct (Cowling and Pierce 1999). In order to preserve native biodiversity and an evolutionarily significant set of pollination guilds, further understanding of the workings of the system and its species is critical. This paper is intended to synthesize current information about the biology and ecology of the long-tongued fly pollination guild and one iconic functional group within the associated floral guild in particular: members of the genus *Pelargonium*. Secondly, a new sub-guild-based classification system

for the varying groups of associated species within the guilds will be suggested, and vulnerability and ecological significance of the guilds will be addressed.

A Description of the Long-Tongued Flies as a Pollination Guild

A paraphyletic group, the moniker 'long-tongued flies' refers to several species across two insect families, the Nemestrinidae, or tanglevein flies, and the Tabanidae, or horseflies, which have evolved extremely elongated mouthparts for the purpose of feeding on nectar stored in the long corolla tubes of specific flowering plant species. Generally, all long-tongued flies are hairy and thick-bodied, with head and thorax at minimum 15 millimeters long, and are distinguished primarily by the unusual length of their proboscides, which are at least as long as or longer than the body (Goldblatt and Manning, 2000); the proportionally-longest proboscis of all insect pollinators belongs to a long-tongued fly, *Moegistorhynchus longirostris,* which has recorded proboscis lengths of up to 95mm, about six times the average body length of the species (Pauw and Stofberg, 2008; Goldblatt and Manning, 2000). Goldblatt and Manning (2000) identified fifteen species between the two families that fall into the long-tongued fly classification, fourteen of which live in South Africa; the fifteenth was discovered in the Himalayas and is thought to have evolved separately. Since the publishing of their 2000 paper, more fly species that could possibly fall under this classification have been identified or named, but require further research to be definitively included in this guild. While there are other nectar-feeding fly species with elongated mouthparts in South Africa, such as those in the family Bombyliidae, they do not possess the same level of extreme specialization in terms of proboscis length that the Nemestrinidae and Tabanidae show, and are thus not included in this guild.

Taxonomic classification of the flies in the family Tabanidae has been difficult, due to the obscurity or variability in discriminating taxonomic features in many species (Morita 2008). The

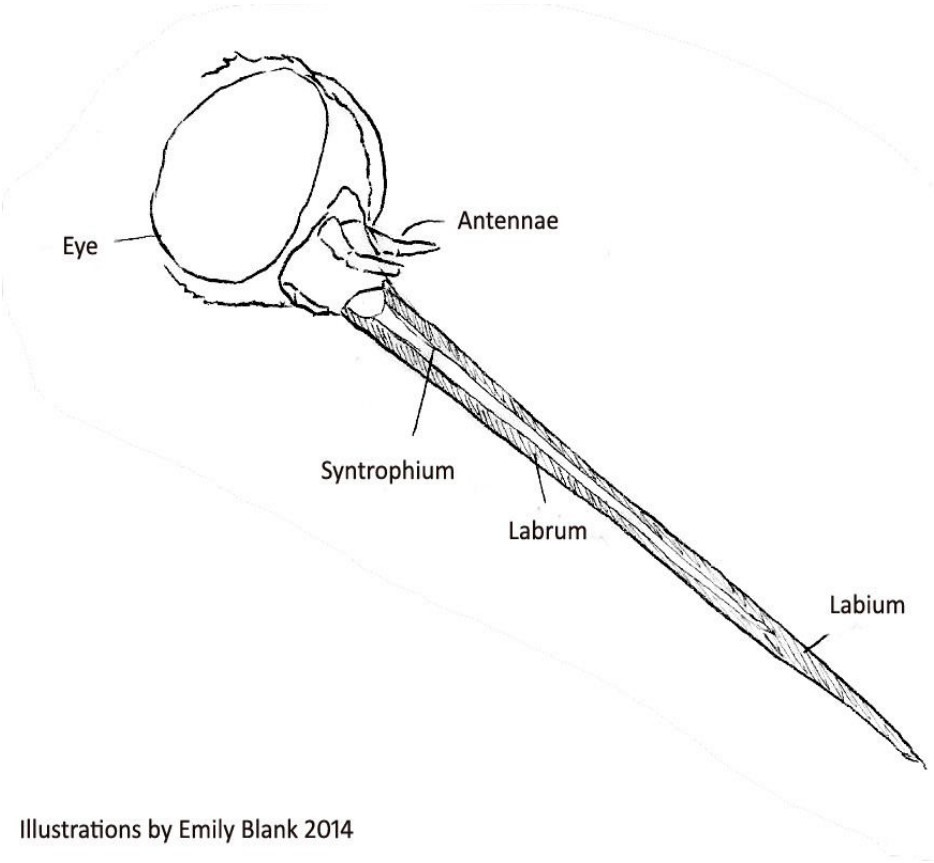
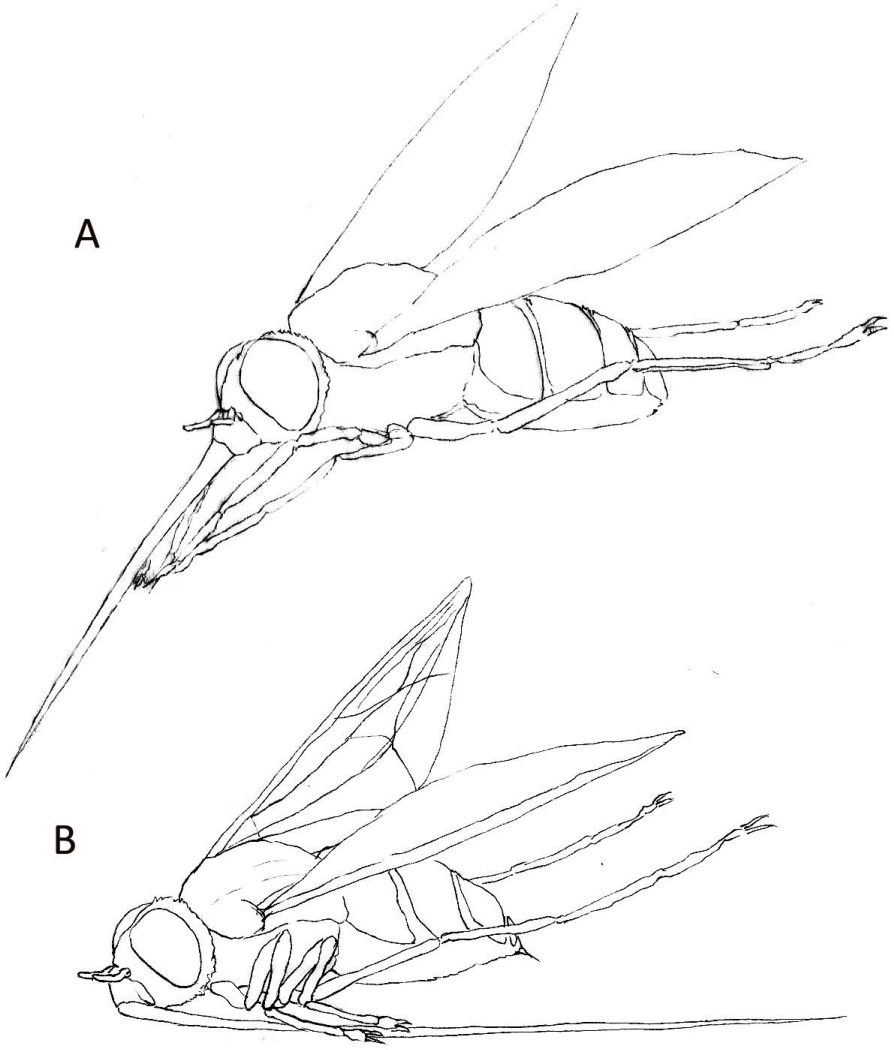


Figure 1. Hypothetical illustration of long-tongued fly mouth parts.

current classification of long-tongued flies in Tabanidae is based on Oldroyd's (1957) scheme. All long-tongued flies found in the family Tabanidae belong to the subgenus *Philoliche philoliche* within the genus *Philoliche* (Morita 2008). All *Philoliche* species are restricted to southern Africa save for one, *Philoliche longirostris* of Asia, which has the longest proboscis of the Tabanidae species (Goldblatt and Manning 2000). The proboscides of long-tongued flies in the genus *Philoliche* consist mainly of an extended labium, a basal organ in blood-feeding Dipteran lineages, including the Tabanidae, which normally sheathes sharper parts used to cut flush in order to draw blood for consumption. In long-tongued species, the labium has been specialized for nectar-feeding rather than blood-sucking. However, many female long-tongued flies remain capable of blood-sucking in order to gain nutrients and increase fecundity, as other tabanid fly females do. Females in the wild having been observed tucking their long labium to the side and using a smaller, sharper organ called the syntrophium to “bite” and extract blood from mammals (Morita, 2008; c.f. Fig. 1.). Males have not been observed drinking blood and are assumed to be entirely nectar-dependent, like the males of the short-tongued tabanids; these male horseflies do not need the additional nourishment for reproduction.

Nemestrinid long-tongued flies make up the remainder of long-tongued fly species in South Africa. The major genus of long-tongued flies in this family is *Prosoeca*, with other species found in the genera *Moegistorhynchus* and *Stenobasipteron*. The nemestrinid flies also differ from the tabanid flies in their mouthpart functionality; nemestrinid long-tongued flies use their mouthparts exclusively to feed on nectar, and their labiums have poor mobility, limited to tucking the proboscis under their ventral side during rest and flight (Karolyi et al. 2012). Additionally, nemestrinid long-tongued fly larvae are believed to be plant parasites based on the anatomy of the flies' ovipositors. These are retractable and likely used for boring holes in plant stems in which they lay their eggs (Karolyi et al. 2012), though the specific plant species which act as hosts in this process are unknown. Both families of long-tongued flies, however, seem to have undergone convergent evolution in their mouthparts, with tabanids merely retaining the ancestral blood-sucking characteristics. The largest long-tongued flies are found in this group, and are able to feed on larger and deeper-tubed flowers than *Philoliche* flies where their territories overlap (Pauw and Stofberg 2009; Newman et al. 2014). Nemestrinidae and tabanidae also adopt different postures during flight, with Nemestrinid flies tucking their proboscides beneath their bodies during flight and lifting their legs above their bodies (Pauw and Stofberg 2009), while Tabanid flies lower their legs and leave their proboscides extended in front of them (Anderson and Johnson 2008; c.f. Fig.2.).

The morphology of many long-tongued fly species varies geographically in terms of color and proboscis length (Morita 2008), both interspecifically and intraspecifically (Goldblatt and Manning 2000; Anderson and Johnson 2008). Some flies have been observed to hover over flowers as they feed from them (Struck 1997), but they are more typically observed gripping the petals of the flowers they visit if landing is possible, continuing to beat their wings while foraging for nectar (Goldblatt 2000) in what may be partial hovering behavior. In cases where flowers are too small to land on or provide no landing platform, however, the flies will just hover (Struck 1997). Hovering can also be observed prior



Illustrations by Emily Blank 2014

Figure 2. Differences in tabanid and nemestrinid flight. **A.** Stereotyped tabanid flight posture with lowered legs and extended proboscis. **B.** Stereotyped nemestrinid flight posture with raised legs and tucked proboscis.

to actual feeding regardless of the possibility of landing, as the flies must maneuver their proboscides into the proper position in order to feed (Anderson and Johnson 2008). On average, the long-tongued flies measure from 15mm to 24mm in length without counting the proboscis (Goldblatt and Manning 2000). All species gain nourishment almost exclusively from nectar-rich flowers, with the aforementioned exception of brooding female Tabanid flies. Except for *Philoliche longirostris*, all long-tongued flies are restricted to South Africa, specifically the Greater Cape Floristic Region (GCFR).

Species of long-tongued flies mostly inhabit the winter-rainfall biotic zone of southern Africa, with the exception of the range of one group extending beyond the GCFR, well east into the summer-rainfall zone. The guild's overall range includes the area along the coast from the Northern Cape Province near the southern border of Namibia to the eastern provinces of KwaZulu-Natal and Limpopo (Goldblatt and Manning 2000; c.f. Fig. 6). Many long-tongued fly species have variable ranges, not always appearing each year in places they were known to inhabit in the past or appearing in locations in which they were previously unobserved (Goldblatt and Manning 2000). Moreover, they are rare and difficult to observe or capture even when specifically sought out (Johnson and Steiner, 1997). Species habitats tend to be divided along seasonal borders for both plant guilds and pollinator guilds, such as areas with a wet-winter season vs. those with a wet-summer season; winter-rainfall areas contain the highest diversity of the flies, with all but 4 observed South African species restricted to these areas (Goldblatt and Manning 2000). The GCFR itself is notable for having an extremely high level of endemic species; the flora is about 67% endemic at the species level (Born et al. 2007). This is attributed to its high environmental heterogeneity and the subsequent variety of niches present (Martinez-Cabrera et al. 2012); the Greater Cape Floristic Region contains complex topography, spatially varying amounts of precipitation, and distinct seasons, likely leading to heightened speciation along habitat gradients within the area (van der Niet and Johnson 2009). Many plant species in the region also have limited dispersal mechanisms, which prevents extensive gene flow and promotes speciation by vicariance (Martinez-Cabrera et al. 2012). The high floral diversity of the region and high number of unique pollination guilds, including bird and rodent pollinators (Cowling and Pierce 1999), oil-collecting bees, and hopliine beetles (Johnson and Steiner 2003), have made it an area of high interest to researchers studying diversification, evolution, and pollination biology.

Associated Floral Guild & *Pelargonium*

Long-tongued flies pollinate many species of flowering plants in at least seven families, with Iridaceae and Geraniaceae having the highest proportion of long-tongued fly pollination. Long-yongued fly pollinators have also been observed pollinating species in the Amaryllidaceae, Orchidaceae, Campanulaceae, Lamiaceae, and Scrophulariaceae as well (Goldblatt and Manning 2000). Species inferred to be pollinated by long-tongued flies, but with no pollination yet observed, can also be found in the Caryophyllaceae and Ericaceae families. Long-tongued flies have been recorded visiting and pollinating over 200 species of flowers in South Africa (Goldblatt and Manning 2000; Karolyi et al. 2012). One hundred and twenty of these species are believed to be pollinated by long-tongued flies exclusively, with up to 90 more possibly exclusive but unconfirmed (Goldblatt and Manning 2000); the term 'rhinomyophilous' has been introduced to describe plants which depend on long-tongued flies for pollination. Additionally, long-tongued flies visit and potentially serve as facultative pollinators to a number of other plant species, visiting any tube-shaped flower accessible to their long proboscis and available within their range (Anderson et al. 2010), including species of Proteaceae (Karolyi et al. 2012). The families containing the highest number of species pollinated by long-tongued flies are the Iridaceae, where they pollinate 10% of species (Goldblatt and Manning 2000), and the Geraniaceae, where 25 % of the genus *Pelargonium* (about 70 species) are known to be pollinated by these flies – the remaining 75% are pollinated by a wide variety of other taxa, including birds, moths, and bees, with the latter being the most common pollinator within the genus (Struck 1997). Depending on the local pollinators present, *Pelargonium* species vary in color, size, and corolla tube depth, with different floral visitor species correlating to different floral morphologies (Struck 1997; Bakker et al. 2005; Röschenbleck et al. 2014.) An example of this floral variety can be seen in Figure 3. *Pelargonium* species are of particular note in the long-tongued fly pollination system for being members of a relatively large genus, composed of about 280 taxa (Bakker et al. 2004;

Figure 3. Examples of *Pelargonium* species displaying different pollination syndromes. From left to right: *Pelargonium fulgidum* (ornithophilous/bird-pollinated), *Pelargonium multicaule* (melittophilous/bee-pollinated), *Pelargonium bowkeri* (phalaenophilous/moth-pollinated), *Pelargonium triandrum* (rhinomyophilous/long-tongued fly-pollinated). Arranged photography from South African National Biodiversity Institute, D. van Rensberg (2011), and L. Ljunqvist (2014).

Röschenbleck et al. 2014), with a large proportion of rhinomyophilous species. The majority of *Pelargonium* are endemic to the Greater Cape Floristic Region of South Africa, which contains 90% of known species within the genus (Röschenbleck et al. 2014); the remaining are found mainly elsewhere in Africa and in Australia (Struck 1997). They are one of thirty or so genera and families that make up the majority of plant diversity in terms of species richness in the Greater Cape Floristic Region (Jones et al. 2013). All *Pelargonium* species are organized into three or four major clades, depending on the data set used and the phylogenetic analysis. Regardless of pollinator, all species across all four clades tend to have dark nectar guides or eyespots, with the exception of about 25 species. These petal markings are thought to be an ancestral character of the genus (Röschenbleck et al. 2014). In addition, most species have enlarged posterior petals (Röschenbleck et al. 2014; also see Fig. 3, Fig. 4). They tend to be shrubby, perennial plants, although some are annual, and the shrubbier species have relatively long-lasting flowers compared to other plant taxa in the local environment (Goldblatt & Manning 1997). The genus exhibits an unusually wide variety of growth forms, including succulent and tuberous species (Bakker et al. 1999). Short floral tubes appear to have been the basal state of the group, but the elongated floral tube has evolved separately multiple times within the genus across all of its major clades, coinciding with the presence of long-tongued flies and a few species of butterfly

(Röschenbleck et al. 2014).

While *Pelargonium* vary in floral morphology depending on pollination syndrome, resulting in many specialized shapes (cf. Fig. 3), all species possess some unifying traits. Generalized *Pelargonium* traits include stipulate leaves, zygomorphic symmetry in the flower, and a backwards spur fused tightly to the pedicel. All species have a long, single floral tube, and a sturdy peduncle which raises the flowers far up above the rest of the plant (Struck 1997). All species possess protruding unilateral anthers and stamens (Struck 1997; see fig. 4). Flower coloration ranges from cream, white, and pale pink to magenta, scarlet and purple, with highly visible nectar guides towards the center of the plant. These conspicuous nectar guides are common in many plants with insect pollinators, and are very important for attracting and directing the long-tongued flies to nectar sources, as the elongated tongues of long-tongued flies make correct orientation for efficient pollination deposition and nectar feeding difficult (Dennis et al. 2011). The nectar guides typically have high contrast against the petals of the flower, and guide the proboscis towards the center of the corolla. The experimental removal of nectar guides in another long-tongued fly-pollinated flowering plant species resulted in a 92% rate of failure in inserting the proboscis by the long-tongued flies (Hansen et al. 2011). In addition to these nectar guides, *Pelargonium* species tend to possess brightly-colored pollen that provides high contrast, as well, ranging from bright orange to violet, which is thought to be another method of directing the pollinator towards the nectar to effect pollination (Goldblatt and Manning 1996; Goldblatt and Manning 1997; Röschenbleck et al. 2014). *Pelargonium* species are exclusively bisexual, with all flowers possessing both stamens and carpels. Lengths of nectar tubes vary both across species and even within species depending on the population (Struck 1997). Blooms last from 2 to 20 days depending on species and location (Struck 1997) before petals are shed. Anthers typically dehisce a day or two after blooming, after which the style is extended and the stigmas begin to unfold

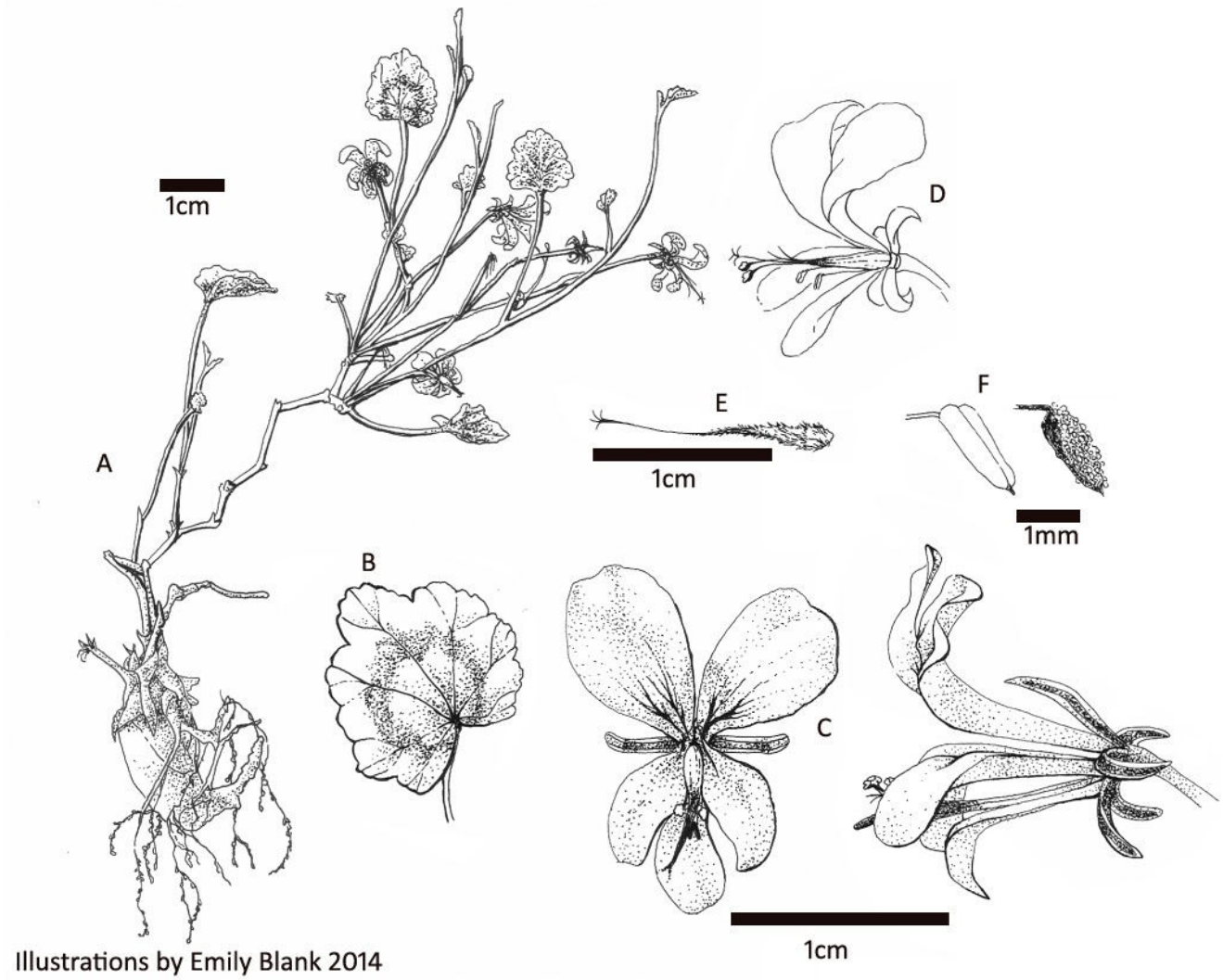


Figure 4. Illustration of *Pelargonium sp. Nov.*, from an unidentified specimen inferred to be a new rhinomyophilous species of *Pelargonium* by its floral characteristics. Note extended declinate anthers, long floral tube and high-contrast veinlike nectar guides. Based on personal observation.

A – Full plate illustration from a live specimen, including roots, tuber, and flowers in various stages of life. **B –** Leaf form (note: drawn from a greenhouse-grown specimen; wild specimens observed had larger leaves.) **C –** Frontal and profile views of flower, including anthers. **D –** Reconstructed image of bisected flower displaying extended anthers, nonextended anthers, and stigma. **E –** Illustration of open stigma. **F –** Anther illustrations. Left: unopened anther. Right: open anther with pollen.

(Goldblatt & Manning 1997; c.f. Fig. 4.). *Pelargonium* species are self-compatible (Struck 1997), but this protandrous system typically reduces autogamous reproduction (Goldblatt and Manning 2000). *Pelargonium* species tend to possess a large volume of high-sugar nectar (Goldblatt & Manning 1997), particularly those visited by long-tongued flies or other large-bodied insect pollinators (Newman et al. 2014); sugar concentrations are within the 20-30% range, and in *Pelargonium,* the dominant sugar is

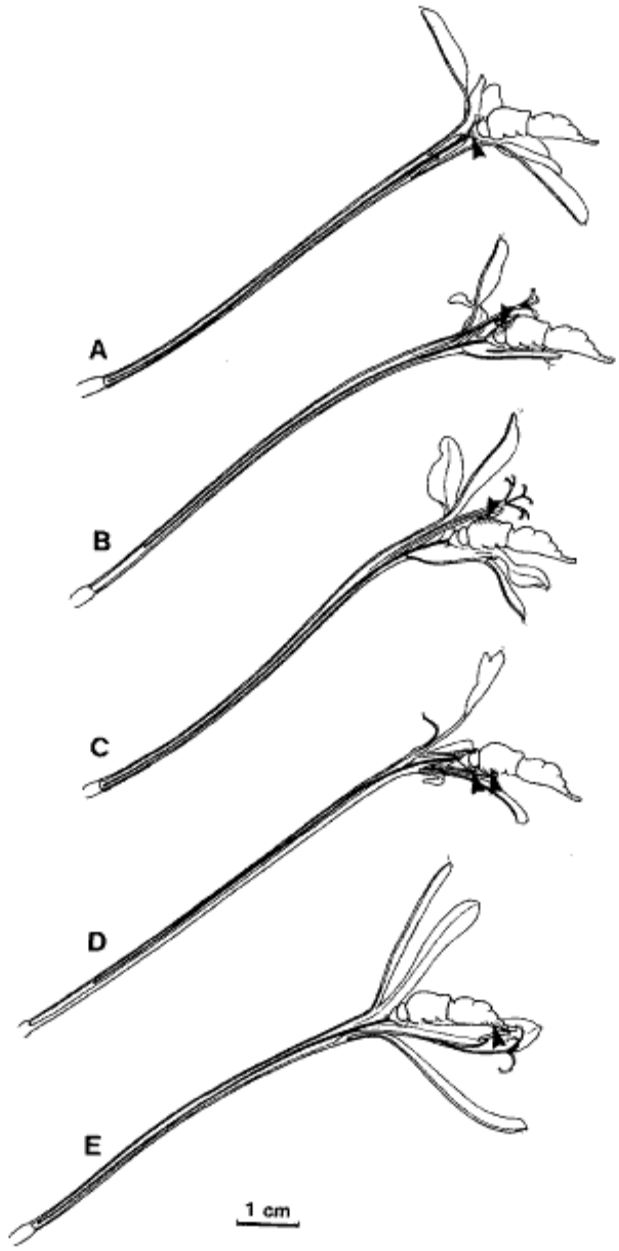


Figure 5. Figure illustrating pollen deposition as copied from Goldblatt and Manning (2000). Darkened areas on flies indicate area of deposition. **A.** Face. **B.** Top of the head. **C.** Top of the thorax. **D.** Bottom of the head. **E.** Bottom of the thorax/abdomen.

hexose rather than the more commonly-dominant sucrose.

All *Pelargonium* species in the rhinomyophilous floral guild share several morphological traits in their flowers, mainly long floral tubes with a large nectar reward at the bottom, high-contrast nectar guides on the petals, extended unilateral stamens and anthers, and a lack of odor (de Merxem et al. 2009; also see illustrations in Figure 4). *Pelargonium* with nectar tubes over 30mm are almost always pollinated by long-tongued flies (Struck 1997). These traits are consistent enough to be used in inferring fly pollination in species without observed visits from flies (Goldblatt & Manning 2000; Bakker et al. 2005). At least one species, *Pelargonium sericifolium*, does not produce any nectar at all, despite having rhinomyophilous characteristics, and appears to be facultatively pollinated by deceit, as it mimics the appearance of local plant species *P. magentum* and *Lapeirousia silenoides*, which do provide nectar for consumption; long-tongued flies have been observed visiting *P. sericifolium* (Goldblatt and Manning 1996; Goldblatt and Manning 2000). As long-tongued flies tend to indiscriminately visit any flower they are able to probe successfully, specific pollen deposition locations on the body of long-tongued

flies seem to have evolved as an adaptation in the floral guild, both to prevent pollen contamination and because the long proboscis of the flies is not a good vessel for pollen transport and often results in pollen loss (Johnson and Steiner 1997; Goldblatt & Manning 1997). There are five general pollen deposition locations on the body of the fly that have been identified across all rhinomyophilous plant species: the top of the thorax, the top of the head, the face, the underside of the thorax, and the under side of the head (Goldblatt & Manning 1997; c.f. Fig. 5.). The zygomorphic structure of the flowers reinforces the correct long-tongued fly positioning required for this precise pollen deposition to work (c.f. Fig. 3, Fig. 4). Additionally, most floral guild species orient their nectar guides towards the center of the flower, guiding the flies into a specific position suitable for both nectar consumption and pollen collection. The number of co-occurring floral sub-guild species in any one location is directly related to the number of different locations on the insect each species exploits for pollen deposition (Goldblatt & Manning 1996); several floral species that all utilize areas on the bottom of the fly are not likely to occur together in one community. *Pelargonium* species in particular tend to have anthers specifically oriented such that pollen is deposited on the underside of visiting flies, due to the declinate positioning of the anthers. Sympatric *Pelargonium* species have varying filament lengths that deposit pollen on different locations on the underside of the fly, minimizing pollen cross-contamination, as seen in *P. incrassatum* and *P. sericifolium* (Goldblatt and Manning 2000).

Pelargonium species not pollinated by long-tongued flies have similarly developed alternative specialized floral forms; Figure 1 shows four different *Pelargonium* floral morphologies for different pollination syndromes. Those pollinated by bees retain an ancestral short corolla tube and possess blotchy eyespots unlike the venous nectar guides displayed by rhinomyophilous species (Röschenbleck et al. 2014); the few species pollinated by birds have red petals and inflated nectar tubes, along with upward-facing anthers to deposit pollen on the bird's forehead (Struck 1997). Butterflies pollinate very few *Pelargonium* species, which usually have medium-length nectar tubes and red petals (Struck 1997).

Moths and hawkmoths pollinate a small percentage of species as well, which have evolved nocturnal pale coloration in their petals and long nectar tubes (Struck 1997).

Similar to the long-tongued flies' proboscides, the nectar tubes of all species within the floral guild vary greatly in length correlated with the pollinator species present. Save for species with very short tubes, *Pelargonium* species' corolla tubes generally show polymorphism varying length over a range of about 20mm on average, with an extreme range of 57mm across different populations of *P. moniliforme* (Struck 1997). The depth and amount of nectar present within any species belonging to the long-tongued fly floral guild may also vary intra-specifically, reflecting the pollinators present in an area where long-tongued flies have become scarce. For example, *Tritoniopsis revoluta*, a member of family Iridaceae typically pollinated by long-tongued flies, has been observed to produce less nectar in the absence of long-tongued flies, or stop producing nectar entirely (de Merxem et al. 2009). This leads to geographic mosaic of morphologies where different populations of the same species have different floral and nectar production phenotypes depending on the pollinator community present (Struck 1997; de Merxem et al. 2009).

Pollination Subguilds within the Long-Tongued Fly Guild Sytem

Within the long-tongued fly pollinator guild and associated floral guild, several distinct and largely non-overlapping polyphyletic populations of long-tongued flies and associated plant taxa can be further distinguished. The members of each respective population share a generalized rhinomyophily syndrome in addition to shared specific morphological features, ranges, and species present. Goldblatt and Manning (2000) organized these groups into three guilds: the *Prosoeca peringueyi* guild, the *Moegistorhynchus longirostris* guild, and the *Prosoeca ganglbaueri* guild. These groupings are based on the fly speces present, the location of their ranges and associated bioclimatic rainfall patterns, and

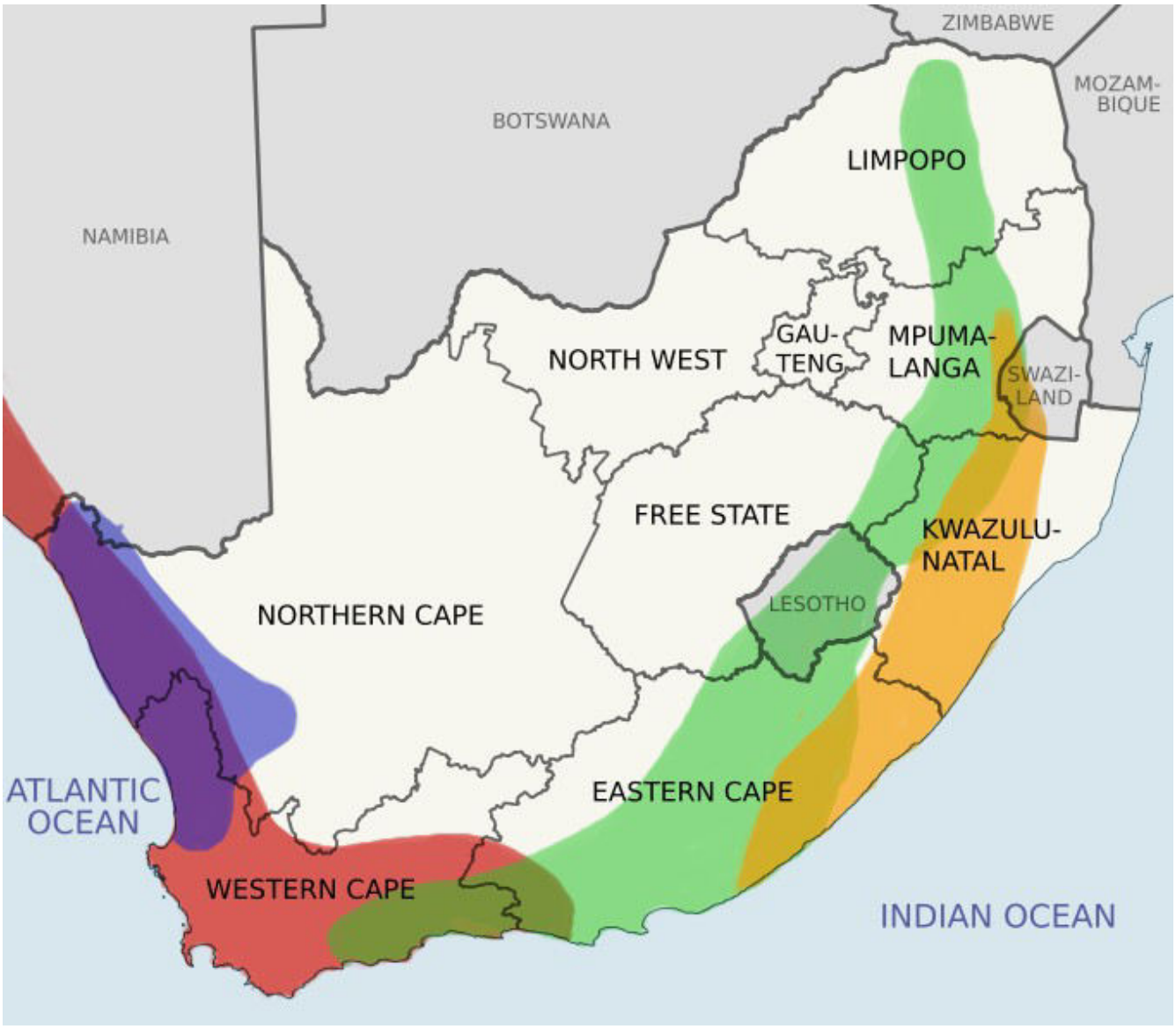


Figure 6. Simplified map of sub-guild ranges based on information and figures from Goldblatt and Manning (2000) and Potgieter and Edwards (2005). Sub-guilds differentiated by color. Blue: *Prosoeca peringueyi* sub-guild. Red: *Moegistorhynchus longirostris* sub-guild. Green: *Prosoeca ganglbaueri* sub-guild. Yellow: Hypothetical *Stenobasipteron wiedemanni* sub-guild.

the characteristics shared by the associated floral guilds within those ranges. Guilds are generally defined as consisting of multiple species exploiting a certain class of resources in a similar way (Goldblatt & Manning 1996). By definition, then, all plants within these guilds are obligate mutualists that depend solely on long-tongued flies for pollination, although they may be receptive to multiple species of long-tongued fly within their respective guild. However, in order to clarify the hierarchy of

relationships within the long-tongued fly pollination system, I suggest redefining these small guilds as sub-guilds in order to avoid confusion between the overall classification of long-tongued fly pollinators and rhinomyophilous plant species, which form the overarching pollinator and floral guild system, and the smaller discrete functional groups identified by Goldblatt and Manning. While rarely used, this system of classification falls in line with the previous definition of guilds and facilitates easier comparisons between features of specific groups within the guilds (see Growns 2004).

One such pollinator sub-guild is the *Prosoeca peringueyi* sub-guild, named for the dominant pollinating long-tongued fly species. The associated floral sub-guild consists of 28 species of plants; both pollinator and floral sub-guilds are located in the Succulent Karoo, a winter-rainfall region extending from the southern Namibian border to Namaqualand and reaching to the northwestern portion of the Western Cape Province (Goldblatt & Manning 1996; c.f. Fig. 6). The floral sub-guild species richness is highest in mountainous areas. The 28 species within the floral sub-guild include six species of rhinomyophilous *Pelargonium,* all of which fall into a single clade; some, but not all, of these *Pelargonium* species display ultraviolet markings on their petals, which likely function as nectar guides (Goldblatt & Manning 2000; Röschenbleck et al. 2014). Pollinating activity occurs in the cooler, wetter months, from late May until early October, when flowers are open during the day. Two species of long-tongued fly are members of this pollinator sub-guild: the titular *Prosoeca peringueyi* nemestrinid fly and an undescribed nemestrinid species (Goldblatt & Manning 2000). Fly visitation most often occurs between 10:30 and 12:30, often at very low density with no more than 5 individual flies appearing in one area at a time (Goldblatt & Manning 1996). Figure 7 shows the flowers of some plant species within this floral sub-guild, which often have bold, dark coloration, with petals usually a deep violet or magenta color and nectar guides cream or white. The *Pelargonium* species within the guild are an exception, possessing pale filaments rather than pale markings on the tepals to act as nectar

Figure 7. Members of the *Prosoeca peringueyi* floral sub-guild. A – *Pelargoinum sericifolium*. B- *Pelargonium incrassatum.* C – *Lapeirousia domitica*. D – *Babiana ecklonii.* Note the pale-colored filaments in the *Pelargonium* species present rather than the pale nectar guides on petals utilized by other taxa in the group. Arranged photography by A. Horstmann (2012), Matija Strlic (2000), F. Forest (2014), and M. S. Ittner (date unknown.)

guides (Goldblatt & Manning 2000). This color patterning is a major defining characteristic of flowers in this floral sub-guild, as it's quite different from the other two identified floral sub-guilds, which typically have paler flowers with dark nectar guides. Floral tubes of plant species within the sub-guild are generally in the 30-60mm range, nearly matching the length of the main pollinating insects' proboscides, which ranged from 20 to 48mm (Goldblatt & Manning 1996). While there is variation in nectar tube length and coloration, flowers within this floral sub-guild generally show strong conformity to the sub-guild traits described, indicating strong selective pressures likely reinforced by the sub-guild of flies that pollinates them.

The *Moegistorhynchus longirostris* sub-guild is a second long-tongued fly pollinator sub-guild. Its range spans the west coast and adjacent interior area of South Africa, from the Orange River through Namaqualand to the Cape Peninsula (Goldblatt & Manning 1997; c.f. Fig. 6) and comprises 20 associated floral sub-guild species, 8 of which are *Pelargonium*. Other species include members of the families Iridaceae and Orchidaceae. While it overlaps geographically with the *Prosoeca peringueyi* sub-guild, large differences in flower color and size minimize the likelihood that flies of one sub-guild could effectively forage on and pollinating the flowers of the other. Flowers of this floral sub-guild are

Figure 8. Members of the *Moegistorynchus longirostris* floral sub-guild. E – *Pelargonium praemorsum*. F – *Pelargonium laevigatum* ssp. *Oxyphyllum*. G – *Aristea spiralis*. H – *Gladiolus angustus.* Aranged photography by I. M Vermeulen (2011), C. Mallek (2010), B. Rutemoeller (date unknown), and M. S. Ittner (date unknown.)

pale, varying in shades of white, cream, and pink, with red dots and stripes for nectar guides, and possessing brightly-colored pollen similar to the pollen found in members of the *Prosoeca peringueyi* sub-guild (see Fig. 8). However, the floral tubes of these species are longer than those of the *Prosoeca peringueyi* sub-guild, measuring between 50mm and 90mm and correlating with the longer tongues of their fly pollinators. There are six to seven fly species in this pollinator sub-guild (Potgieter & Edwards 2005), which have overlapping geographic ranges. Despite this, the morphological differences in the length of their mouthparts and behavioral differences in the time of peak activity reduce competition for nectar, and therefore also reduce the likelihood pollen cross-contamination (Goldblatt & Manning 1997). Nevertheless, male *Moegistorhynchus longirostris* have been observed defending small territories of aggregated nectar-providing plants (Pauw et al. 2009), indicating some level of competition for nectar resources. Species in the floral sub-guild bloom in late spring and early summer, further reducing competition with the geographically overlapping *Prosoeca peringueyi* sub-guild. Pollination often occurs in early morning or late afternoon when conditions are cooler, with a low density of floral visitors appearing within a narrow time frame. This also temporally separates them from pollination activity in the overlapping *Prosoeca peringueyi* pollinator sub-guild.

The third pollinator sub-guild is the *Prosoeca ganglbaueri* sub-guild, which has a range

Figure 9. Members of the *Prosoeca ganglbaueri* floral sub-guild. I – *Pelargonium carneum.* J – *Pelargonium dipetalum.* K – *Tritoniopsis revoluta.* L – *Nivenia stenosiphon*. *N. stenosiphon* is one of the sub-guild species that could potentially be moved into the *Stenobasipteron wiedemanni* sub-guild. Arranged photography by J. Vlok and A. Schlutte-Vlok (2010), D. Victor (date unknown), and N. Helme (2013 + 2006)

stretching from the Limpopo Province to the Klein Swartberg Mountains in southwestern South Africa (c.f. Fig 6). Unlike those occupied by the previous two sub-guilds, the area occupied by *Prosoeca ganglbaueri* sub-guild is very large. It is mostly a summer-rainfall region, with some winter-rainfall areas at the southwesternmost end. Thus, the *Prosoeca ganglbaueri* sub-guild and its associated floral sub-guild overlap spatially only minimally with species in the other two sub-guild systems (Goldblatt and Manning 2000). There is a wide range of *Pelargonium* species that co-occur with this sub-guild, including species from all four clades of the genus. Each *Pelargonium* species in the floral sub-guild possesses white or pink petals with dark nectar guides (Röschenbleck et al. 2014; c.f. Fig. 9). A large number of species from other genera and families also occur within the floral sub-guild. The majority of these plant taxa have deeply pink colored petals with cream-colored markings, although there are some species with an inverse coloration pattern (cream flowers with pink markings), and some species have deep blue petals (Goldblatt and Manning 2000; also see Fig. 9 for examples of color variation). Pollination activity occurs throughout the summer and fall (January to April) and therefore minimizes temporal overlap with pollinator activity in the other two sub-guilds. The pollinator guild comprises four identified species of long-tongued fly: *Prosoeca ganglbaueri, Prosoeca longipennis, Prosoeca robusta,* and *Stenobasipteron wiedemanni,* which have some overlap in their ranges and are

hypothesized to pollinate some of the same species within the floral sub-guild, depending on which fly species is present in the areas where the floral sub-guild plant species occur (Goldblatt and Manning 2000). Despite being visited by one or more species of long-tongued flies, these floral sub-guild species are still considered to be obligately pollinated. They are dependent on long-tongued flies for pollination, and the flowers and nectar resources are inaccessible to other pollinators as long as long-tongued flies are present, as the floral tubes within this sub-guild are too deep for shorter proboscides to reach (de Merxem et al. 2009). This sub-guild has not been as well-documented as the other two guilds, and in fact, research by Potgieter & Edwards (2005) suggests splitting this guild into two, and making *Stenobasipteron wiedemanni* a separate pollinator sub-guild. This fourth sub-guild system would include all of the blue-petaled floral taxa, as well as some geographically local pink and white taxa, all with dark spots and tube lengths varying from 22 to 39mm. *Stenobasipteron wiedemanni* would be the sole long-tongued fly pollinator in this proposed fourth pollinator sub-guild (Potgieter & Edwards 2005). The *S. wiedemanni* sub-guild has no associated *Pelargonium* floral sub-guild members, but 19 species from other families, including Lamiaceae, Iridaceae, and Acanthaceae.

The number of plant species in each floral sub-guild far outweighs the number of fly species that pollinate them; as stated above, long-tongued flies are generally non-specific foragers and will visit any tubular flower that they can access and that also has the suite of traits associated with the rhinomyophilous syndrome (Pauw et al. 2009). While the majority of flowering plant species in the guild system are visited by just one species of fly, due to differences in geographical range, period of activity, and proboscis length amongst flies, there are some that are pollinated by more than one species of long-tongued fly, and most of the fly species visit multiple plant species (Goldblatt and Manning 2000). There are few exclusive species pair interactions in this mutualistic system (Pauw et al. 2009). Rather, there is a more general obligate relationship between the floral and pollinator sub-guild

members; the long-tongued fly pollination guild system is a collection of mutualistic interactions between similar paraphyletic groups with homoplasious traits. The flowering plant species visited by long-tongued flies come from at least seven families comprising over 200 rhinomyophilous species, but all of them possess similar coloring, nectar guide arrangement, and corolla tube depth range, regardless of taxonomic classification. Despite this observed floral guild species richness, the guild system that has evolved between long-tongued flies and rhinomyophilous flowers is so specialized as to allow multiple floral guild species obligately exploiting the same pollinator to grow and bloom in the same area with little to no pollen cross-contamination. This is due to spatio-temporal separation in pollination activity, variation in tube depth and proboscis length (Goldblatt and Manning 1996), and differential pollen placement on the pollinating fly (Goldblatt and Manning 1997). Some of the pollinator sub-guilds have overlapping geographical ranges, but there is little competition between fly species, as each is locally specialized for the flowers of its associated floral sub-guild and may be physically unable to access the nectar of others, either due to spatio-temporal differences in activity or morphological differences in the corolla tubes of the floral sub-guild species (Goldblatt and Manning 1997). Fly species with shorter proboscides are unable to reach nectar in long-tubed flowers; species with longer proboscides have low maneuverability and generally receive less nectar from smaller, shorter-tubed flowers, making these flowers an inefficient food source (Anderson and Johnson 2008; Pauw et al. 2009). Additionally, flowers visited by long-tongued flies with proboscides that do not match the length of their floral tubes have significantly lower reproductive success and seed set (Anderson and Johnson 2008).

Coevolution and Speciation within the Guild System

The long proboscides of the long-tongued flies and the deep floral tubes of the plant species

they pollinate show clear reciprocal coadaptations, varying in accordance to which species are present in the area (Goldblatt and Manning 2000, Newman et al. 2014). These reciprocal traits are correlated in a predictable fashion, i.e. a plant with a 60mm floral tube can be inferred to be pollinated by a long-tongued fly with a proboscis of similar length, even when other environmental factors, such as altitude or climate, are included as cofactors that might also affect morphological variation(Anderson and Johnson 2008). This correlation between proboscides and floral tubes has been consistently observed across multiple plant families, despite the flies' tendency to visit any flower which they can probe successfully (Pauw et al. 2009; Hansen et al. 2011) and the tendency of some species within the floral guild to adapt to the pollination requirements of other pollinator species when long-tongued flies are not present. The process by which this shift occurs is not clear. A shift to bee pollination was observed in some populations of the typically rhinomyophilious *Tritoniopsus revoluta,* which involved the discovery of a population with nectar tubes reduced to almost half the typical length, found next to another population, separated by a small transition zone, which had individuals of normal length (de Merxem et al. 2009). The retention of matching proboscis lengths and nectar tube depths amidst this variation suggests that species within the guild system are exerting mutual continuous selective pressure on these associated traits. When the relative rarity of many long-tongued fly species (Cowling and Pierce 1999; Goldblatt and Manning 2000) and their variability in both foraging and range is considered, the proportion of flowers that have shown local adaptation to compete for their use as pollinators seems remarkable. However, while there is an obligate dependence of the floral guild on the pollinator guild and vice versa, it appears that many members of the guild system are flexible at the species or population level, due to high adaptability of coupled traits in both the *Pelargonium* (Struck 1997) and the long-tongued flies. Species within the floral guild utilize the most efficient and reliable pollination mechanism available in their local environment, and are equipped to adapt relatively quickly to changes in that environment should the most efficient competitor change (Anderson and

Johnson 2008; de Merxem et al. 2009; van der Niet et al. 2014). When long-tongued fly pollinators are absent in the community, nectar has been observed to well up in floral guild species with especially narrow floral tubes to the point that shorter-tongued pollinators can access it (Goldblatt and Manning 1996). Individuals with shorter nectar tubes allow the welled-up nectar to be accessed more easily by short-tongued pollinators (de Merxem et al. 2009). This adaptive variation has also been observed within the pollinator sub-guilds. *Prosoeca peringueyi,* for example, has a proboscis measuring between 20 and 45mm. The length of the proboscis varies geographically and is correlated with the length of the floral tube in the associated sub-guild plant species in the local community, suggesting that shifts in proboscis length are due to selection pressure exerted by visited plant species within the community (Goldblatt and Manning 1996; Anderson and Johnson 2008). It is unclear whether the variation in these traits is genetically fixed among populations or an example of phenotypic plasticity, particularly within the floral guild, as this type of plasticity is unlikely in the long-tongued flies. As genotypic shifting for adaptation would be remarkable, I suggest a reciprocal transplant study using replicated phenotypes from different populations of a particularly flexible polymorphic group of one or more species in order to clarify the genetic basis and maintenance of this morphological variation.

It is important to note that the matching parts within the guild system, the proboscides and nectar tubes, rarely match exactly, as there are multiple pollinator species and multiple associated floral guild species in most populations, the majority of which are highly labile. Over time, selection operates on the proboscides and nectar tubes, leading to convergence in pair mutualisms. In the flexible obligate mutualism present in the long-tongued fly guild system, mismatches persist due to continuing variation in foraging behavior, community floral composition and diversity, and adaptability of the involved species, preventing complete reproductive isolation within the floral species (van der Niet et al. 2014). Studies by Anderson et al. (2010) showed that mutualistic pollination traits are often mismatched in a

predictable fashion depending on the number and complexity of specialized traits. This refers to features such as specialization of organs, i.e. the lengthening of the proboscis in long-tongued flies, or changes in appearance and behavior adapted specifically to increase efficiency within the mutualism, such as the extended anthers and directional nectar guides within the floral sub-guilds. Low complexity and magnitude of traits, such as having only a small increase in proboscis size or nectar tube and nothing else altered, matches the organisms or mismatches them in favor of the insect pollinator, i.e. having a proboscis longer than the floral tube that enables nectar foraging without pollination. High complexity and magnitude of traits, such as having a variety of specific traits like nectar guides, extended anthers, and extremely elongated nectar tubes, results in a mismatch favoring the plant, i.e. having a corolla tube longer than the proboscis of the pollinator fly species enables more pollen deposition than one that is shorter (Anderson et al. 2010). This pattern is thought to occur due to the fact that highly-specialized insect pollinators are often still able to visit several different plant species, whereas highly-specialized plant species will have a much heavier reliance in their specific mutualistic pollinator. Thus, plants must maintain an 'advantage' at high trait magnitudes in order to continue to benefit from the relationship. The extreme elongation of the proboscis of *Moegistorhynchus longirostris* is an example of a highly complex specialized trait: the bright pollen, high-contrast nectar guides, and declinate anthers of rhinomyophilous *Pelargonium* species are an example of a high number of specialized traits, as they all appear to be used in order to attract the pollinator or increase the pollinator's efficiency (Newman et al. 2014). Species within the long-tongued fly guild system have a high number of specialized traits, leading to a mismatch favoring the plant (Anderson et al. 2010). This mismatch can possibly be explained by the fact that, if the fly was favored, a proboscis just slightly longer than the corolla tube of the visited flower might be able to access the nectar without coming into close enough contact for optimal pollination deposition, thereby reducing the benefits of the mutualism for the plant. Alterations in the surrounding community structure also may have an

effect, as the exaggeration in floral tube length seemed to be related to the number of other plants visited by the pollinator fly (in the case of Anderson et al.'s (2011) study of *Prosoeca ganglbaueri*). If there were a variety of other, shorter-tubed plants upon which *P. ganglbaueri* also foraged, I hypothesize that a plant species depending solely on *P. ganglbaueri* for pollination might display more extreme elongation in its corolla tube. This provides the plant with a competitive advantage over the other floral sub-guild species, likely to better attract the long-tongued fly, as having such a long floral tube guarantees that only *P. ganglbaueri* will be able to access the nectar reward and thus presents a secure food source. Increased frequency of pollinator visits generally leads to increased pollination. Having a long proboscis also leads to longer handling times when attempting to feed on shorter-tubed plants, making foraging at such plants inefficient and thus reducing competition amongst plant species for the pollinator (Anderson et al. 2010). Again, this merits further research, possibly by observing the nectar tube length and seed set of a floral guild species in a varied rhinomyophilous plant community over time; a reciprocal transplant study could also be applicable here. Extreme differences between tube length and proboscis length can become detrimental for both plant and pollinator, leading to little pollen attachment and/or small nutritional benefits to the fly (Pauw et al. 2009), and a study by Anderson and Johnson (2008) suggests that strongly mismatched communities of long-tongued flies and plants are in a transitional state due to recent shifts in long-tongued fly foraging range or recent changes in assemblages of plant species.

The possible fitness benefits due to the correlation of specialized traits mentioned above, like a guaranteed nectar resource or guaranteed pollination vector, likely maximize survival and reproductive gains in species populations of both components of the pollination guild system, thus leading to consistent reciprocal adaptation across multiple sites (Anderson and Johnson 2008; Newman et al. 2014). Having a large nectar source reachable only by a pollinator with a long proboscis provides that

pollinator with a consistent food source and provides the plant with a consistent pollinator. As there is competition within the plant community for preference by the fly pollinator, it's likely that species within the community which encourage more efficient foraging by the pollinator by way of having particularly deep floral tubes, encouraging the long-tongued fly to specialize in return (Pauw and Stofberg 2009). This more specialized system would tend to have more reproductive success, though this merits further testing, perhaps by comparing seed set of different populations of a floral species which have varying degrees of trait matching with their pollinator. As mentioned earlier, there is a predictable mismatch in the pollination syndrome where the floral tube is slightly longer than the proboscis of the visiting fly (Anderson et al. 2010). This is likely due to the fact that pollinators are often more generalized than the plant species, which may depend exclusively on one pollinator species (Anderson et al. 2010); the long-tongued fly pollinator sub-guilds and their associated plant species are no different, as long-tongued fly species are greatly outnumbered by the plant species depending on them for pollination and variably forage other plants in the community (Goldblatt and Manning 2000; Pauw et al. 2009; Anderson et al. 2010). This can result in asymmetrical selection – the floral sub-guilds, due to their dependence, adapt to the pollinator sub-guilds (Newman et al. 2014).

This uneven selection can also apply to the long-tongued flies, as pollinators other than long-tongued flies are known to visit rhinomyophilous plant species in some geographical areas (Newman et al. 2014). In cases where the long-tongued flies are no longer present in their former range, species of specialized plants may adapt to other pollinators in the area by allowing nectar to well up in their floral tubes. This allows shorter-tongued insects, such as bees or beetles, to access it (de Merxem et al. 2009). Selective pressure may also cause the floral tube to narrow in order to push nectar towards the top of the floral tube for easier access (Goldblatt and Manning 1996). Similarly, certain species of flowers within the range of *P. longipennis* maintain a concentration and volume of nectar that fits the syndrome

of both long-tongued flies and bees (Newman et al. 2014). Bet-hedging strategies such as this within the floral sub-guilds, in addition to the possibility of self-pollinating in the absence of pollinators (van der Niet et al. 2014), are not uncommon. Pauw and Stofberg (2009) referred to this as "diffuse selection:" a group of organisms engaged in reciprocal selection with another group of organisms, or multiple groups. In other words, selection pressures from multiple other species affect a particular focal species, resulting in a more generalized adaptive phenotype. Diffuse selection may explain the commonality of bet-hedging strategies in the associated floral guild and the genus *Pelargonium*'s retained capability for self-pollination; diffuse selection and its associated polymorphisms adapt many species in the system for a variety of different pollination situations. Furthermore, diffuse selection may also explain why extreme specialization of floral tubes and proboscides appears to only occur in some species and some locations. In order for coevolution to continue, it seems that both pollinator and plant must be present and still exerting continuous and intensive selection pressure on one another. Areas where selection pressures between the two groups has either become one-directional or disappeared completely, due to changes in pollinator location or the community makeup, were termed "cold spots" by Pauw et al. (2009). Their studies showed that, in one community, members of the plant species *Lapeirousia anceps*, typically pollinated by *Moegistorhynchus longirostris*, had developed nectar tubes much shorter than the proboscides of *M. longirostris.* As this means *M. longirostris* would be an inefficient vehicle for pollen, it seems likely that *L. anceps* was no longer coevolving with that pollinator. These are contrasted with the actively-coevolving "hot spots," where *M. longirostris* and *L. anceps* had closely-correlated proboscis lengths and nectar tube lengths, suggesting continuing mutalism and coevolution. These alterations in adaptation and pollination system occur on a fine geographic scale according to shifts in pollinator behavior and morphology (Newman et al. 2014) and pollinator distribution (van der Niet et al. 2014), as well as gene flow between populations facing different selection pressures, which may prevent trait equilibrium from being reached (de Merxem et al.

2009). Abiotic environmental factors may also play a role, as low temperatures, strong winds, and high elevations may constrain the evolution of a very long proboscis in fly species due to body size restrictions (Anderson and Johnson 2008); the magnitude of these effects on long-tongued fly species is a possible topic to pursue in research, perhaps by observing morphological variation within a species across several ecologically similar but geographically distinct populations.

The high intraspecies polymorphism and propensity for adaptive shifts within this guild system have led to a suggested geographic mosaic theory of coevolution (Pauw et al. 2009), which states that species engaged in mutualisms form a mosaic of different populations of varying levels of interdependence and mismatch within their collective ranges. Coevolution occurs only in those populations where the interacting organisms continue to exert high selection pressure on one another regardless of other environmental factors; Anderson and Johnson (2008) suggested that in simpler plant and pollinator communities, therefore, higher rates of coevolution may be observed. The variable corolla tube lengths within individual *Pelargonium* species were speculated to be the result of such a mosaic by Struck (1997). The geographic mosaic theory may also account for morphological differences across populations of *P. ganglbaueri*, in which the presence of multiple accessible flowering species was hypothesized to constrain proboscis elongation (Anderson and Johnson 2008); the same theory has been applied to constrained proboscis growth within other long-tongued fly species (Goldblatt and Manning 1996; Johnson and Steiner 1997; Pauw et al. 2009). The geographic mosaic model has recently been suggested as one primary cause behind the expansive floral radiation within the GCFR (van der Niet et al. 2014). These pollination community mosaics may provide insight into the early evolutionary stages of speciation, as pollinator shifts can contribute to reproductive isolation and drive divergent selection for more extreme specialized traits (van der Niet et al. 2014).

The high rate of polymorphism within the long-tongued fly guild system, as well as the

propensity for adaptive shifts in pollinators among the floral sub-guild species, appears to be novel amongst pollination systems. The high rate of plant speciation within the GCFR is believed to be at least in part pollinator-driven (van der Niet and Johnson 2009). While having diversified into many species, the long-tongued fly pollination guild's associated floral sub-guilds appear to have evolved into a more generalized syndrome correlated with frequent shifts in pollinator distribution, which in turn may reflect the outcome of competition and variation within this diverse floral community. Studying the long-tongued fly pollinator guild system, then, along with particularly flexible floral sub-guild members such as *Pelargonium* species, provides a useful model of the process of coevolution and the role that correlated reciprocal coevolution may play in this (Pauw et al. 2009). A wide variety of studies still remain to be done on the system in order to further elucidate the evolutionary process by which members of the guild system become specialized: for example, whether or not the morphological variation is environmentally plastic or genetically determined remains unclear, suggesting a need for ecological genetics and reciprocal transplant studies. Additionally, the amount of time it takes for a population within the floral guild to shift from long-tongued fly pollination to another mode of pollination also merits a long-term observational study. Further research is also of particular importance due to the threat of habitat fragmentation to the sustainability of the pollination guild system (Rodger et al. 2004); much of the Cape region of South Africa has already been heavily altered by agriculture and urbanization (Hannah et al. 2005). Long-tongued flies are considered keystone species where they occur due to the high number of plant species that depend on them (Goldblatt and Manning 1996). Though many of their dependent species display significant lability, the presence or absence of any one fly species would likely still have a serious effect on its codependent sub-guild. Conducting further studies on the workings of the guild system's coadaptations will play an important part in conserving the species therein.

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